A New Cascade Frog of the Subgenus *Odorrana* from Peninsular Malaysia

Masafumi Matsui^{1*} and Ibrahim Jaafar²

¹Graduate School of Human and Environmental Studies, Kyoto University, Sakyo-ku, Kyoto 606-8501, Japan ²Biological Sciences Program, School of Distance Education, Universiti Sains Malaysia, 11800 USM, Penang, Malaysia

We describe a new species of cascade frog of the genus *Rana*, from west Malaysia. *Rana monjerai*, new species is a medium-sized frog of the subgenus *Odorrana* (SVL of males, 38–43 mm; of one female, 75 mm), and is distinguished from all other members of this subgenus by the combination of: white lip stripe, dorsolateral fold, full web on the fourth toe, vomerine teeth, gular vocal pouch and relatively large tympanum in males, no dorsal marking, no clear light spots on rear of thigh, first finger subequal to second, finely tuberculated dorsum, and unpigmented ova. The significance of finding this species from peninsular Malaysia is discussed.

Key words: cryptic species, Rana, new species, Southeast Asia, taxonomy, zoogeography

INTRODUCTION

Along mountain streams in subtropical and tropical regions of East to Southeast Asia, there are small to medium-sized, long-legged ranid frogs represented by species like *R. narina* Stejneger, 1901 from the Ryukyu Archipelago of Japan; *R. livida* (Blyth, 1856) from China to Myanmar (now proved to be a composite of allied species, see Bain *et al.*, 2003); and *R. hosii* Boulenger, 1891 from the Malay Peninsula to Borneo (Bourret, 1942; Liu and Hu, 1961; Taylor, 1962: Inger, 1966; Maeda and Matsui, 1989; Fei *et al.*, 1991).

These cascade frogs have been treated variously as a distinct genus, *Odorrana* (Fei *et al.*, 1991), or as subgenera *Eburana, Odorrana*, and *Chalcorana* of the genus *Rana* (Dubois, 1992). However, a recent phylogenetic analysis of mtDNA sequences revealed their monophyly within the genus *Rana* (Matsui *et al.*, 2005), and suggested use the subgeneric name *Odorrana*, which precedes other names (Fei *et al.*, 1991).

Through the extensive field surveys in East and Southeast Asia, many species of *Rana* (*Odorrana*) have been described in this decade (Matsui, 1994; Fei *et al.*, 2001a,b; Orlov *et al.*, 2003; Bain and Nguyen, 2004; Stuart and Bain, 2005). Of these, most species from Southeast Asia have been reported from Vietnam and Laos, and no new *Rana* (*Odorrana*) has been reported from western Malaysia. Only *R. hosii* was known from this region (Berry, 1975), although Taylor (1962) included Perak in the range of *R. livida*.

On a recent trip to Gunung (=Mount) Jerai, in the northern part of the western coast of West Malaysia, the junior author collected five specimens of *Rana* (*Odorrana*) super-

* Corresponding author. Phone: +81-75-753-6846; Fax : +81-75-753-6846; E-mail: fumi@zoo.zool.kyoto-u.ac.jp doi:10.2108/zsj.23.647 ficially resembling *R. hosii*, which the senior author (Matsui, unpublished data) had obtained at higher elevations on the same mountain. Later examination of these specimens, however, revealed that they are clearly different from *R. hosii* in the presence of gular pouches in males. Further study of the specimens by consulting with a recent review of the group (Bain *et al.*, 2003) led us to conclude that they represent a new species, which is described below.

MATERIALS AND METHODS

A field survey was made between 4 and 10 June 2005 along the Teroi River on the northern slopes of Gunung Jerai, on the western coast of West Malaysia. We collected specimens by hand, anesthetized them with chloroform, and fixed them in 10% formalin. For preserved specimens, we took the following 16 body measurements, mainly following Matsui (1984), to the nearest 0.1 mm with dial calipers: snout-vent length (SVL); head length (HL), from tip of snout to hind border of angle of jaw (not measured parallel with the median line); eye length (EL); tympanum diameter (TD); head width (HW); internarial distance (IND); interorbital distance (IOD); upper eyelid width (UEW); lower arm length (LAL); first finger length (1FL), from junction of first and second fingers to tip of first finger; second finger length (2FL), distance from junction of first and second fingers to tip of second finger; third finger disk diameter (3FDW); fourth toe disk diameter (4TDW); hindlimb length (HLL); tibia length (TL); foot length (FL), from proximal end of inner metatarsal tubercle to tip of fourth toe. Character definitions follow Bain et al. (2003). For diagnosing the new species, we examined 35 specimens of *R*. hosii from Malay Peninsula, including four from Gunung Jerai (KUHE 15291-15292, 15371-15372; KUHE=Graduate School of Human and Environmental Studies, Kyoto University).

SYSTEMATICS

Rana monjerai sp. nov. (Fig. 1)

Diagnosis

A medium-sized form of *Odorrana*; female 75 mm, males from 38 to 43 mm in snout-vent length (SVL); distinct



Fig. 1. Male holotype of *Rana monjerai* [USM (Universiti Sains Malaysia) 422, SVL=43.2 mm]: (A) dorsal view; (B) ventral view; (C) profile; (D) ventral view of right foot. Scale bar: 5 mm.

dorsolateral fold present; first finger subequal to second; toe webbing full on the fourth toe; vomerine teeth present; gular vocal pouch present in males; tympanum large in males, 51–66% of eye length, much smaller in female; dorsum finely tuberculated; upper lip broadly striped white; dorsal marking absent; rear of thigh without light spots; ova unpigmented.

Holotype

USM (Universiti Sains Malaysia) 422 (original field number IJJW 070605-2), an adult male from the Teroi River on Gunung Jerai, State of Kedah, West Malaysia (5° 47'N, 100° 27'E, alt. 720 m a.s.l.). Collected on 7 June 2005 by I. Jaafar and L.-H. Wong.

Paratypes

USM 423 (Original field number IJJW 070605-3), USM 424 (original field number IJJW 070605-4), USM 426 (original field number IJJW 070605-6), and USM 429 (original field number 070605-9), three adult males and an adult female, same data as for the holotype.

Description of holotype

Body moderately slender; head triangular, longer than wide; snout straight dorsally, rounded at tip, projecting beyond lower jaw, rounded in profile; eye large, longer than snout; canthus distinct; lore vertical, deeply concave, nostril nearer to tip of snout than to eye; internarial distance much wider than interorbital; latter much narrower than upper eyelid; pineal spot visible, slightly anterior to line connecting anterior corners of orbits; tympanum conspicuous, more than one-half of eye diameter and separated from eye by one-sixth of tympanic diameter; vomerine teeth in short, oblique groups, beginning from anterior to a line connecting anterior corners of choanae and extending posteromedially, groups equidistantly separated from each other and from choanae by about half length of each group; tongue deeply notched, without papilla; paired subgular vocal sacs form gular pouches at corners of throat; vocal openings just inside commissures of jaws.

Forelimb stout; fingers unwebbed; first finger subequal to second; fourth longer than first; tips dilated into disks having circummarginal grooves, the outer two wide, width 2.5 times width of phalanges; disk of third finger slightly less than half diameter of tympanum; distinct nuptial pads, cream in colour and velvety in structure, covering dorsal and median surfaces of the first finger from its base to distal edge of the subarticular tubercle.

Hindlimb rather long, about two times SVL; heels overlapping when limbs are held at right angles to body; tibiotarsal articulation of adpressed limb reaching beyond tip of snout; disks of toes narrower than those of two outer fingers; third toe shorter than fifth; toes fully webbed, to disc in first to third and fifth toes; fourth toe moderately widely webbed to base of disc on inner and outer edges; webs thick, not crenulate; subarticular tubercles very prominent, oval; inner metatarsal tubercle distinct, oval, one-third length of first toe; outer metatarsal tubercle absent; no tarsal fold.

Dorsum finely granular with glandular dorsolateral folds and flat supratympanic folds; side of trunk coarsely granular; chest and abdomen smooth.

Color in formalin

Dorsum grayish brown without distinct marking; lore with a dark marking below canthus; upper lip broadly banded white, without dark marking; tympanum dark brown, encircled by light brown, with blackish-brown rim; dorsolateral fold edged with dark; flank dark brown; limbs marked dorsally, with dark brown crossbars; rear of thigh indistinctly mottled with dark and light spots; lower lip white without marking; abdomen and ventral surfaces of hindlimb whitish; throat scattered with pigmentation of melanophores along inner side of lower lip and around vocal pouches; foot webbing dark brown.

Measurements of holotype

Measurements (in mm) in preservative: SVL 43.2; HL 17.1; EL 7.4; TD 4.1; HW 14.0; IND 4.8; IOD 3.5; UEW 4.5; LAL 21.5; 1FL 5.8 (right hand) and 5.9 (left hand); 2FL 5.8 (right hand) and 5.6 (left hand); 3FDW 1.9; 4TDW 1.8; HLL 80.4; TL 26.4; FL 23.0.

Variation

A single female (SVL=75.3 mm) is larger than four males (38.4-43.1 mm, mean \pm SD= 41.88 ± 2.32 mm). The small number of samples limited statistical comparisons, but some dimensions relative to SVL seem to be sexually dimorphic. Males have larger values relative to SVL than females in head width (32.0-34.1% vs. 31.9%), head length (38.8-40.4% vs. 37.9%), upper eyelid width (10.2-10.4% vs. 9.3%), eye length (15.8-17.1% vs. 13.6%), and tympanum length (8.4-10.9% vs. 5.3%).

Lengths of eye and snout are subequal in the female. Pineal spot is located slightly posterior to line connecting anterior corners of orbits in one male. Tympanum is separated from eye by one-third and three-fifths of its diameter in one male and the female, respectively. First finger is slightly longer than second in some specimens but vice versa in others, and in one specimen, the relationship is reversed in the right and left hands. In the female, disk of third finger is four-fifths diameter of tympanum, and vomerine tooth groups are separated from each other and from choanae by about one-third the length of each group. Dorsolateral fold is feeble in two males and is distinct in anterior one-third in the female. One male has weak whitish asperities on lower lip, on dorsolateral fold, and on tibia. Individuals are fairly uniform in coloration and pattern of markings, but upper lip is scattered with pigmentation of melanophores in two males, and flank is posteriorly marked with small dark spots in one male. In the female, dark brown color on flank is restricted to anterior one-fifth. From the photographs taken of three males in life, the dorsal color varies from green with dark brown spots to dark brown with irregular green markings. One male has brownish flecks on throat.

Eggs

Diameter of an ovum from a female is 2.3 mm. The eggs are entirely cream in colour

Comparisons

Rana monjerai superficially resembles R. hosii, and both of these species have been collected from Gunung Jerai, although neither simultaneously nor syntopically (see below). A subadult female of R. hosii (SVL=69.4 mm) had a dusky venter, unlike R. monjerai with white venter. Adult females of *R. hosii* from other localities on the Malay Peninsula had greater SVL (80.2-95.3 mm, mean=85.2 mm, n=6) than R. monierai (75.3 mm), and all had a dusty venter (Matsui, unpublished data). Rana hosii is larger than R. monjerai also in males (SVL=44.5-53.2 mm, mean=48.0 mm, n=17, and 38.4-43.2 mm, mean=41.9 mm, n=4, respectively). Males of the two species differ from each other more clearly than females, because R. hosii lacks the pair of gular pouches that are present in R. monjerai. In this regard, R. monjerai is more similar to R. livida than to R. hosii, both of which are assigned to the subgenus Odorrana (Matsui et al., 2005). It is not easy to allocate ranine species from Asian regions to Odorrana, but some species from China (Fei et al. 1991; Fei et al., 2005) and other species defined as the R. chloronota complex by Bain et al. (2003) and subsequent

Table 1. Measurements of 16 characters in *Rana monjerai*. SVL is given as mean±1SD, in mm); medians of ratios (R) of other characters to SVL (in %) are followed by ranges in parenthesis. See Materials and Methods for character abbreviations.

Sex	n	SVL	RHW	RHL	RLAL	RTL	RFL
Male	4	41.9±2.32	33.1	39.5	49.8	65.5	54.8
		(38.4–43.2)	(32.0–34.1)	(38.8–40.4)	(49.5–52.6)	(61.1–66.4)	(53.2–57.6)
Female	1	75.3	31.9	37.9	49.8	63.5	55.6
Sex	n	RHLL	RIND	RIOD	RUEW	REL	RTD
Male	4	198.0	10.7	8.2	10.3	16.5	9.4
		(186.1–207.3)	(10.0–11.1)	(7.0-8.4)	(10.2–10.4)	(15.8–17.1)	(8.4–10.9)
Female	1	192.3	10.1	8.4	9.3	13.6	5.3
Sex	n	R1FL	R2FL	R3FDW	R4TDW		
Male	4	13.1	13.1	4.4	3.6	-	
		(11.5–13.5)	(12.5–13.6)	(4.2–5.4)	(3.4–4.2)		
Female	1	14.6	13.1	4.6	3.6		

authors (Orlov *et al.*, 2003; Bain and Nguyen, 2004) are considered to be members of *Odorrana*. Although Stuart and Bain (2005) refrained from placing their new species in *Odorrana*, we tentatively include them in this subgenus.

Rana monjerai differs from other species of the subgenus Odorrana in the following characteristics (data from Bain et al., 2003; Bain and Nguyen, 2004; Fei, 1999; Fei et al., 1991, 2005; Inger, 1966; Maeda and Matsui, 1999; Stuart and Bain, 2005; Stuart et al., 2005): (1) Presence in males of a pair of gular pouches [absent in R. andersonii Boulenger, 1882; R. exiliversabilis Li, Ye, and Fei in Fei, Ye, and Li, 2001; R. grahami Boulenger, 1917; R. hainanensis (Fei, Ye, and Li, 2001); R. hmongorum Bain, Lathrop, Murphy, Orlov, and Ho, 2003; R. jingdongensis (Fei, Ye and Li, 2001); R. junlianensis (Huang, Fei, and Ye in Fei and Ye, 2001); R. kuangwuensis Liu and Hu in Hu, Zhao, and Liu, 1966; R. margaretae Liu, 1950; R. versabilis Liu and Hu, 1962; R. wuchuanensis Xu in Wu, Xu, Dong, Li, and Liu, 1983; and R. hosii]. (2) Possession of white lip (lip not white in R. bacboensis Bain, Lathrop, Murphy, Orlov, and Ho, 2003; R. bolavensis Stuart and Bain, 2005; R. heatwolei Stuart and Bain, 2005; R. lungshengensis Liu and Hu, 1962; R. orba Stuart and Bain, 2005; R. schmackeri Boettger, 1892; R. sinica Ahl, 1927 "1925"; R. tiannanensis Yang and Li, 1980; and R. trankieni Orlov, Ngat, and Ho, 2003). (3) Presence of dorsolateral fold [absent in R. chloronota (Günther, 1876); R. hejiangensis Deng and Yu, 1992; R. ishikawae (Stejneger, 1901); R. livida; and R. lungshengensis. Fold indistinct and interrupted in R. amamiensis Matsui, 1994; R. narina; R. supranarina Matsui, 1994; R. swinhoana Boulenger, 1903; and R. utsunomiyaorum Matsui, 1994]. (4) Non-enlarged tympanum in male [large tympanum, >0.66 times eye length in R. banaorum Bain, Lathrop, Murphy, Orlov, and Ho, 2003; R. graminea Boulenger, 1900; R. megatympanum Bain, Lathrop, Murphy, Orlov, and Ho, 2003 (including R. tabaca Bain and Nguyen, 2004); R. morafkai Bain, Lathrop, Murphy, Orlov, and Ho, 2003; and some R. orba]. (5) First and second fingers subequal (first finger shorter than second in R. daorum Bain, Lathrop, Murphy, Orlov, and Ho, 2003; R. iriodes Bain and Nguyen, 2004; and R. sinica. Second finger shorter than first in R. amamiensis, R. bacboensis, R. banaorum, R. bolavensis, R. chloronota, R. hainanensis, R. heatwolei, R. hejiangensis, R. hmongorum, R. junlianensis, R. kuangwuensis, R. livida, R. margaretae, R. megatympanum, R. morafkai, R. narina, R. orba, R. schmackeri, R. supranarina, R. swinhoana, R. tiannanensis, and R. utsunomiyaorum). (6) Full web on the fourth toe (not full in *R. anlungensis* Liu and Hu in Hu, Zhao, and Liu, 1973; R. leporipes Werner, 1930; R. bolavensis, R. daorum, R. iriodes, R. orba, R. supranarina, and R. utsunomiyaorum). (7) Absence of outer metatarsal tubercle (present in R. nasuta Li, Ye, and Fei in Fei, Ye, and Li, 2001, and R. exiliversabilis; sometimes present in R. heatwolei). (8) Absence of "serration" along upper lip (present in R. exiliversabilis, R. nasuta, and R. versabilis). In addition, Rana leporipes is reported to have a characteristically white supratympanic fold, which is not seen in R. monjerai.

Additionally, several other ranine species superficially resemble the new species, but cannot be assigned with certainty to *Odorrana* in the absence of phylogenetic evidence. Of these, *R. archotaphus* Inger and Chan-Ard, 1997 and *R.* khalam Stuart, Orlov, and Chan-Ard, 2005 possess an outer metatarsal tubercle, unlike *R. monjerai. Rana archotaphus* also differs from *R. monjerai* in lacking a full fourth toe web.

Range

Known only from the type locality, the Teroi River on Gunung Jerai, western coast of West Malaysia.

Natural history

This species was found perching on rocks and sand along mountain streams about 720 m above mean sea level in montane myrtaceous forest (Gregory-Smith, 1994) on Gunung Jerai. The breeding season seems to be later than early June, because a single female collected has fully mature eggs in her ovaries. Associated anuran species observed include *Limnonectes blythi*, *L. laticeps*, and *R.chalconota. Rana hosii* has been recorded (Matsui, unpublished data) on Gunung Jerai at localities higher in altitude (1050–1100 m) than the type locality of *R. monjerai.*

Etymology

The specific name derives from the type locality, Gunung Jerai. It is also a dedication to the Kedah State Government, the Kedah Forestry Department, and the Malaysian Forestry Department, which are the governing bodies of the Gunung Jerai Forest Reserve and whose kind permission and support made the trip possible.

DISCUSSION

Because members of *Rana* (*Odorrana*) possess distinct digital disks, some of them were once treated as *Hylarana* (*e.g.* Boulenger, 1920). It was Fei *et al.* (1991) who proposed a distinct genus, *Odorrana*, to encompass *R. livida* and other Chinese relatives. Dubois (1992), however, relegated *Odorrana* as a subgenus of *Rana*, while proposing many other new subgenera, such as *Eburana* and *Chalcorana*, in this genus. He placed *R. narina* and *R. livida* in *Eburana*, and *R. hosii* in *Chalcorana*.

These studies were done exclusively on the basis of morphology, and phylogenetic relationships among the genera treated by Fei *et al.* (1991) and the subgenera treated by Dubois (1992) were poorly known. Recently, Matsui *et al.* (2005) reconstructed the phylogenetic relationships among *Eburana, Odorrana,* and *Chalcorana hosii* by an analysis of mitochondrial 12S and 16S rRNA gene sequences, and confirmed the monophyly of these taxa as the subgenus *Odorrana* of the genus *Rana.*

Recent progress in the elucidation of species diversity in *Odorrana* is surely the most splendid among systematic studies of East and Southeast Asian anurans. Many new species have been found, long after the last revisions in these regions (Southeast Asia in general: Bourret, 1942; China: Liu and Hu, 1961; Japan: Nakamura and Uéno, 1963; Thailand: Taylor, 1962; Peninsular Malaysia: Berry, 1975; Borneo: Inger, 1966).

In China, seven species, now assigned to *Odorrana*, were described between 1950 and 1983 (Liu, 1950; Liu and Hu, 1962; Hu *et al.*, 1966, 1973; Yang and Li, 1980; Wu *et al.*, 1983), and five more new species were added in 2001 (Fei and Ye, 2001; Fei *et al.*, 2001a, b). These include several cryptic species once treated as a single species. From

the Ryukyus, Japan, Matsui (1994) described three cryptic species related to *R. narina*, while Bain *et al.* (2003) more recently revised *Odorrana* and clarified the taxonomic status of important species described earlier (*R. livida, R. chloronota, R. sinica, R. leporipes*). They also described six cryptic species allied with *R. chloronota* from Vietnam. Orlov *et al.* (2003) and Bain and Nguyen (2004) each described one new species from Vietnam. Most recently, Stuart and Bain (2005) added three new species allied with *R. mega-tympanum*, treated as *Odorrana* by Bain *et al.* (2003), from Laos and Vietnam, while relegating one Vietnamese species (*R. tabaca*) as a synonym of another (*R. megatympanum*), both described by Bain *et al.* (2003).

From these recent spectacular discoveries of many cryptic species of Rana (Odorrana) in Southeast Asian countries, it is not surprising to find one in peninsular Malaysia. Rana monjerai would easily have been confused with R. hosii or R. livida (Taylor, 1962). Indeed, R. hosii occurs at higher elevations than does R. monjerai on Gunung Jerai. Because the co-occurrence of more than one species of Odorrana at a single locality has been reported in Vietnam and Laos (Bain et al., 2003), a similaly syntopic distribution might also be expected on Gunung Jerai. Future intensive field surveys, as well as close examination of many more specimens both morphologically and genetically, will clarify whether this is the case. In conducting such studies, it is important to adequately examine the range of intraspecific variation so as to avoid increasing the number of synonymies.

ACKNOWLEDGMENTS

We thank L.-H. Wong for help in the field and A. Tominaga for help in the laboratory. We also express our gratitude to the Kedah State Government, the Kedah Forestry Department and the Malaysian Forestry Department for permission and logistical support. This study was partially supported by Universiti Sains Malaysia Short Term Grant No. 304/PJJAUH/ 634167 to I. Jaafar.

REFERENCES

- Bain RH, Nguyen QT (2004) Herpetofaunal diversity of Ha Giang Province in northeastern Vietnam, with descriptions of two new species. Am Mus Novit 3453: 1–42
- Bain RH, Lathrop A, Murphy RW, Orlov N, Ho TC (2003) Cryptic species of a cascade frog from Southeast Asia: taxonomic revisions and descriptions of six new species. Am Mus Novit 3417: 1–60
- Berry PY (1975) The Amphibian Fauna of Peninsular Malaysia. Tropical Press, Kuala Lumpur
- Boulenger GA (1920) A monograph of the South Asian, Papuan, Melanesian, and Australian frogs of the genus *Rana*. Rec Ind Mus 20: 1–126
- Bourret R (1942) Les batraciens de l'Indochine. Mem Inst Oceanogr l'Indochine Hanoi 6: 1–547
- Deng QX (1992) A new species of the genus *Rana* from China. J Sichuan Teach Coll (Nat Sci) Nanchong 13: 323–327
- Dubois A (1992) Notes sur la classification des Ranidae (Amphibiens Anoures). Bull Mens Soc Linn Lyon 61: 305–352
- Fei L (Ed) (1999) Atlas of Amphibians of China. Henan Science and Technology Press, Zhengzhou

- Fei L, Ye CY (Ed) (2001) The Color Handbook of the Amphibians of Sichuan. China Forestry Press, Beijing
- Fei L, Ye CY, Huang YZ (1991) Key to Chinese Amphibia. Chongqing Branch Science and Technology Literature Press, Chongqing
- Fei L, Ye CY, Li C (2001a) Descriptions of two new species of the genus *Odorrana* in China (Anura: Ranidae). Acta Zootaxon Sinica 26: 108–114
- Fei L, Ye CY, Li C (2001b) Taxonomic studies of *Odorrana versabilis* in China II. Descriptions of two new species (Amphibia: Ranidae). Acta Zootaxon Sinica 26: 601–607
- Fei L, Ye CY, Jiang JP, Xi F (2005) An Illustrated Key to Chinese Amphibians. Sichuan Publ Group Sichuan Publ House Sci Technol, Chengdu
- Gregory-Smith R (1994) An altitudinal study of birds of Gunung Jerai, Kedah. Malay Nat J 47: 417–424
- Hu SC, Djao EM, Liu CC (1966) A herpetological survey of the Tsinling and Ta-Pa Shan region. Acta Zool Sinica 18: 57–89
- Hu SC, Djao EM, Liu CC (1973) A survey of amphibians and reptiles in Kweichow Province, including a herpetofaunal analysis. Acta Zool Sinica 19: 149–178
- Inger RF (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zool 52: 1–402
- Liu CC (1950) Amphibians of Western China. Fieldiana Zool Mem 2: 1–400
- Liu CC, Hu SC (1961) Chinese Tailless Batrachians. Science Press, Beijing
- Liu CC, Hu SC (1962) A herpetological report of Kwangsi. Acta Zool Sinica 14 Suppl: 73–104
- Maeda N, Matsui M (1989) Frogs and Toads of Japan. Bun-ichi Sogo Shuppan, Tokyo
- Maeda N, Matsui M (1999) Frogs and Toads of Japan, Revised Edition. Bun-ichi Sogo Shuppan, Tokyo
- Matsui M (1984) Morphometric variation analyses and revision of the Japanese toads (Genus *Bufo*, Bufonidae). Contrib Biol Lab Kyoto Univ 26: 209–428
- Matsui M (1994) A taxonomic study of the *Rana narina* complex, with description of three new species. Zool J Linn Soc 111: 385–415
- Matsui M, Shimada T, Ota H, Tanaka-Ueno T (2005) Multiple invasions of the Ryukyu Archipelago by Oriental frogs of the subgenus *Odorrana* with phylogenetic reassessment of the related subgenera of the genus *Rana*. Mol Phylogent Evol 37: 733–742
- Nakamura K, Uéno SI (1963) Japanese Reptiles and Amphibians in Colour. Hoikusha, Osaka
- Orlov NL, Nguyen NL, Thu CH (2003) A new species of cascade frog from North Vietnam (Ranidae, Anura). Russ J Herpetol 10: 123–134
- Stuart BL, Bain RH (2005) Three new species of spinule-bearing frogs allied to *Rana megatympanum* Bain, Lathrop, Murphy, Orlov and Ho, 2003 from Laos and Vietnam. Herpetologica 61: 478–492
- Stuart BL, Orlov NL, Chan-Ard T (2005) A new cascade frog (Amphibia: Ranidae) from Laos and Vietnam. Raffles Bull Zool 53: 125–131
- Taylor EH (1962) The amphibian fauna of Thailand. Univ Kansas Sci Bull 43: 265–599
- Wu L, Xu RH, Dong QD, Li DJ, Liu JS (1983) A new species of *Rana* and records of amphibians from Guizhou Province. Acta Zool Sinica 29: 66–70
- Yang DT, Li SM (1980) A new species of the genus *Rana* from Yunnan. Zool Res Kunming 1: 261–264

(Received January 20, 2006 / Accepted April 5, 2006)